# Skeletal-Muscular Mechanisms of the Larva of *Lucilia sericata* (Meigen) in Relation to Feeding Habit[1]

(Diptera: Calliphoridae)

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Despite the recognized medical and economic importance of the Diptera, scant work has been undertaken on the functional anatomy of the head in immature forms. The mouth hooks and associated structures of cyclorrhaphous larvae are prerequisite to the damage incurred by these insects in the course of aberrant feeding activity (Menees, 1962). In the past this feeding behavior has been employed as a surgical technique for removal of necrotic tissue on humans but under such conditions, *Lucilia sericata* (Meigen) readily invades adjacent healthy tissue (Haub and Miller, 1933). Cutaneous myiasis of domestic animals, especially sheep and cattle results from infestation of wounds by the immature stages of this same species (Hall, 1948) and *L. sericata* has been implicated in episodes of sheep strike in both England and Wales (Zumpt, 1965). In contrast, Donahoe (1937) has shown *L. sericata* to be a significant economic pest when invading drying fruits in certain parts of California.

Dealings with the cephalopharyngeal structure of immature cyclorrhaphous Diptera have been mainly taxonomic in nature. A few works have described the associated musculature (Hewitt, 1910; Snodgrass, 1924; Miller, 1932; Ludwig, 1949; Hartley, 1963; Roberts, 1969, 1970) but a general paucity of such information exists. The purpose of this study was to describe the cephaloskeletal muscles of the third instar larva of *L. sericata* and to detail the function of each muscle or muscle group in the process of feeding.

## Materials and Methods

A laboratory colony of *L. sericata* (Meigen) was maintained according to the method of Dorman et al. (1935). Swine liver was employed as both a protein source and oviposition medium for adult females. Adults were otherwise maintained on sucrose and water.

Larval morphology was studied primarily by means of dissection.

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histological sections were made where necessary for verification of detail. Study of the cephalopharyngeal apparatus was facilitated by treatment of the head with 10% KOH at room temperature for 24-hours. Material for histological sections was double embedded in paraffin after primary embedding in methyl-benzoate-celloidin solution. Serial sections were made at 10 to 20 microns, and muscular tissue was stained using Milligans trichrome staining method (Humason, 1967).

Material for dissection was injected with and stored in Bouin's fixative (Humason, 1967). Methylene blue was used as a contrast stain during subsequent dissections.

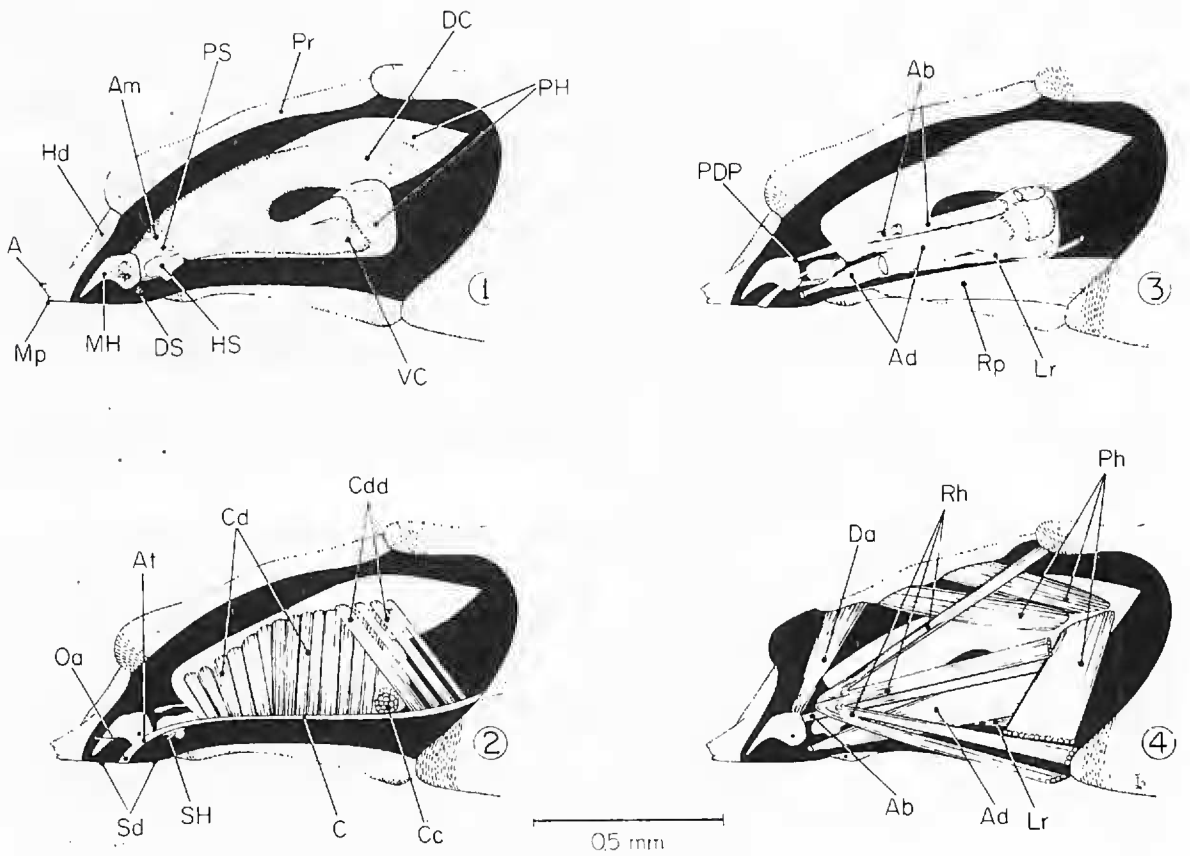
## Results

External Anatomy. The third instar larva of *L. sericata* exhibits anatomical configuration similar to that of other cyclorrhaphous larvae (Figs. 1 and 2). The prothorax (Pr) is the first apparent anterior segment, but partially invaginated into it lies the head (Hd). Ventrally, the head exhibits an oral aperture (Oa), anterior to which lie the paired mouth hooks (MH) and posterior to which lies the liguloid region. The stomal disc (Sd), completely surrounding the oral aperture, bears small grooves or canals which aid in conduction of extra-orally digested food to the oral aperture. Other external features of the head include the paired sensory papillae represented anterodorsally and anteroventrally by the antennae (A) and maxillary palpi (Mp) respectively.

Cephalopharyngeal Skeleton. This structure is bilaterally symmetrical in *L. sericata* and is composed of three sections: the basal sclerite, the intermediate sclerite, and the mouth hooks region (Figs. 1 and 2). The posterior-most and largest section is the double-winged basal sclerite, appearing laterally as a prostrate U-Shaped structure. The arms of the U are formed by the dorsal (DC) and ventral cornua (VC) each of which diverges posteriorly and is further extended in this direction by a chitinous phragma that serves as a site for muscle attachment. Right and left halves of the basal sclerite are joined together anterodorsally and anteroventrally by small sclerotized arches.

The intermediate sclerite, or midsection, articulates with the preceeding basal sclerite by means of the arch-shaped hypostomal sclerite (HS). Over the median arch of this latter structure passes the cibarium (C), while immediately below the cibarium and anterior to the hypostomal sclerite lie the smaller subhypostomal sclerites (SH). The two parastomal sclerites (PS), apparent as small, slightly upturned rods projecting from the anterolateral surface of the basal sclerite, are also considered a part of the intermediate sclerite (Miller, 1932).

The third section, or mouth hook region consists of the paired




Figs. 1-4. Left lateral view, internal anatomy of head and prothorax in *Lucilia sericata*. Legend: A, antennal palp; Ab, abductor of the mouth hook; Ad, adductor of the mouth hook; Am, atrial membrane; At, atrium; C, cibarium; Cc, constrictor of the cibarium; Cd, dilator of the cibarium; Cdd, diagonal dilator of the cibarium; Da, dilator of the atrium; DC, dorsal cornu; DS, dentate sclerite; Hd, head; HS, hypostomal sclerite; Lr, liguloid retractor; MH, mouth hook; Mp, maxillary palp; Oa, Oral aperature; PDP, posterodorsal process of mouth hook; Ph, protractor of the head; PH, phragma; Pr, prothorax; PS, parastomal sclerite; Rh, retractor of the head; Rp, retractor of the prothorax; Sd, stomal disc; SH, sub-hypostomal sclerite; VC, ventral cornu. Fig. 1. Cephalopharyngeal skeleton. Fig. 2 Internal view of cephalopharyngeal skeleton showing cibarial musculature. Fig. 3. Musculature of the mouth hooks. Fig. 4. Composite view of all cephalopharyngeal musculature *in situ*.

mouth hooks (MH), each of which articulates with the anterior face of the hypostomal sclerite, and the dentate sclerites (DS). Likewise, in this section, arises the atrial membrane (Am) which begins at the anterior limit of the oral aperture and expands posterodorsally and laterally to connect with the anterodorsal ridge of the basal sclerite.

Spanning the ventral length of the cephalopharyngeal skeleton is the anterior portion of the alimentary canal. The oral aperture (Oa) forms its anterior limits, while between the oral aperture and the opening of the salivary duct, at the posteroventral base of the hypostomal sclerite, lies a post-oral cavity or atrium (At). From the salivary duct to the posterior limit of the cephalopharyngeal skeleton is located the cibarium. Ventrally, in this latter structure, is the cibarial filter which is composed of numerous longitudinal T-shaped ridges.

Musculature. Four functional groups of muscles were found in the head-thoracic region: (1) muscles involved in functioning of the atrium and liguloid region, (2) muscles of the cibarium, (3) muscles functioning in movement of the mouth hooks, and (4) muscles utilized for locomotory or taxis movement of the larval head-thorax.

Group one (Figs. 3 and 4) is composed of the liguloid retractor (Lr) muscles and the dorsal dilators of the atrium (Da). Originating from the phragma of the ventral cornu on either side, each liguloid retractor inserts upon a small, straplike sclerite, the liguloid arch, which lies between the paired mouth hooks. The dorsal dilators of the atrium descend from either side of the dorsal prothoracic midline and fuse to form a single median muscle which inserts (by apodeme) upon the dorsal surface of the atrium.

The cibarial muscles (Fig.2) exist as three separate subgroups of the group two muscles: (1) the dilators of the cibarium (Cd), consisting of 14 separate muscles, each originating from the ventral surface of the dorsal cornu and inserting upon the upper surface of the cibarium, (2) the diagonal dilators of the cibarium (Cdd); 4 separate muscles each originating median to those of subgroup (1) and descending caudad to insert upon the dorsal surface of the cibarium, and (3) the constrictor muscle of the cibarium (Cc); existing as a single large muscle transversing the distance between the two ventral cornua, and dorsal to the cibarium.

Adduction and abduction of the mouth hooks is performed by the paired group three muscles (Fig. 3), a separate pair for each process. The abductors of the mouth hooks (Ab), like the adductors (Ad), originate from the phragma of the ventral cornu of either side. Each abductor muscle inserts directly upon the posterodorsal process (PDP) of its corresponding mouth hook, whereas each adductor muscle connects to its respective dentate sclerite. A ligamentous connection exists between each dentate sclerite and the mouth hook adjacent to it.

Group four muscles (Figs. 3 and 4) are the largest muscles in size, and can be divided into three separate subgroups. The first subgroup is the protractors of the head (Ph). Members of this subgroup are bilateral and consist of 2 dorsal muscles and a single ventral muscle. Both of the dorsal muscles originate dorsolaterally on the prothoracic wall, whereas the ventral muscle originates ventrolaterally on the prothoracic wall. All members of this group insert upon the phragma of the dorsal cornu. The second subgroup is the retractor muscles of the head (Rh) which are bilaterally symmetrical. Members of this subgroup originate from various points along the pro-mesothoracic junction, while all members of each side insert upon the parastomal sclerite. The retractors of the prothorax (Rp), the third subgroup, consists of 10 muscles, all of which originate ventrally at the junction of the metathorax and abdomen. Two external muscles and 3 internal muscles exist on either side of the dorso-ventral midline.

## Discussion

Adult females of *L. sericata* oviposit upon recently expired animal flesh but generally avoid excessively putrified material. Upon hatching, early first instar larvae feed in close proximity to the oviposition site while older larvae disperse over the feeding medium (Barnard, personal observation). In all three larval instars of this fly, digestion occurs extra-orally by means of both amylase containing saliva and proteolytic enzymes passed off in larval excreta (Hobson, 1932b). Large numbers of larvae usually feed within small areas of substrate and this activity further enhances the extra-oral digestive process.

Linear movement in *L. sericata* takes place in a fashion similar to that described by Roberts (1971) for other cyclorrhaphous larvae: Waves of muscle contraction, commencing posteriorly and traveling anteriorly, terminate at the head or anterior end of the larva. Each wave of contraction ends with elevation and protraction of the head. Elevation involves contraction of the intersegmental muscles and contraction of retractors of the prothorax (Rh), extension or protraction of the head occurs by means of contraction of the protractors of the head (Ph). Taxis or steering changes are made possible by unilateral contraction of the protractors of the head (Ph).

Feeding activity in the larva of *L. sericata* begins with the head elevated and the mouth hooks in the abducted position (Ab). The head is lowered until the stomal disc contacts the feeding substrate following which the mouth hooks are adducted (Ad) and driven into crevices of the feeding substrate surface. Contraction of the liguloid retractor muscles (Lr) draws posteriad the liguloid region and allows saliva to flow forward from the salivary duct opening and out of the oral aperture. Maceration of the substrate occurs as the retractors (Rh) and protractors of the head (Ph) contract and relax synergistically, while the mouth hooks are held in the adducted position. This entire process is aided by the large retractor muscles of the prothorax (Rp). Ingestion of the semiliquid material produced by this process begins with relaxation of the liguloid retractor muscles causing the oral aperture to diminish in size. Subsequent contraction of the dilators of the atrium (Da) apparently induces an internal pressure deficit whereby food is brought through the oral aperture into the atrium. Grooves present on the stomal disc, all of which circulate toward the oral aperture, also aid in conducting food into the digestive tract. From the atrium, food moves into and out of the cibarium by alternating contraction and relaxation of the cibarial muscles (Cd, Cdd, Cc). No valves are present in the cibarium and the brownish food mass can be observed through the larval cuticle as it flickers back and forth during transit through this structure.

A structure present in many other cyclorrhaphous larvae, and one of uncertain function, is the cibarial filter. In *L. sericata* the cibarial filter runs the length of the ventral portion of the cibarium and appears similar in cross section to that of *Calliphora vomitoria* (L.) (Roberts, 1970). Speculation centers upon its functioning as a filtering and draining mechanism whereby excess liquid and small food particles are diverted back to the atrium and egested rather than passing through the alimentary canal (Roberts, 1970). Baumberger (1919) suggested the cibarial filter to be characteristic of mycetophagous larvae only. However, this structure exists in *L. sericata* and Hobson (1932a) demonstrated the rearing of normal larvae of this species on aseptic media. The ingestion of bacteria by larvae of *L. sericata* may be unavoidable in the course of normal feeding. It may also be, as demonstrated by Levinson (1960), that ingested bacteria fulfill the dietary requirements of many cyclorrhaphous larvae, but in a facultative rather than obligatory sense (i.e. the larvae are fortuitous feeders). In any event, definitive evidence for the function of the cibarial filter in cyclorrhaphous larvae is lacking. Furthermore it seems futile to label this structure as being characteristic of either saphrophagous or mycetophagous forms until a greater understanding of the dietary requirements of species in this group is acquired.

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